

Seed dormancy and persistence of *Acacia berlandieri* and *Leucaena pulverulenta* in a semi-arid environment

M. K. Owens*, R. B. Wallace† & S. Archer‡

* Texas Agricultural Experiment Station, Uvalde, Texas

† The Nature Conservancy, Santa Fe and ‡ Department of Rangeland Ecology and Management, Texas A&M University, College Station, Texas, U.S.A.

(Received 12 April 1993, accepted 9 June 1993)

Seed longevity of the leguminous shrubs *Acacia berlandieri* and *Leucaena pulverulenta* was evaluated under field conditions at the soil surface and at 3–5 cm depth. Abiotic influences on seed longevity and dormancy were investigated by comparing seeds maintained at 5°C with seeds experiencing fluctuating day/night temperatures (40°C/20°C vs. 50°C/30°C) under dry and moist conditions. *Acacia* seed demonstrated no dormancy and initial germinability was >82% in the laboratory. Viability of *Leucaena* seed was >97%, but seed coat dormancy limited germination to <7%.

Persistence of *Acacia* seeds in the soil seed bank varied with depth. After 42 days the viable seed population of *Acacia* was reduced by 10 and 80% for surface and buried seeds, respectively, and no viable seeds were present after 3.5 months of burial. In contrast, *Leucaena* seeds on the soil surface exhibited no significant decline in viability over 60 days and attrition of buried seed was <11%. After 3.5, 6 and 12 months of burial, 86, 81 and 71% of the *Leucaena* seeds dispensed remained viable, but the hard seed coat limited germination to 5, 2 and 0%, respectively. Loss of dormancy of *Leucaena* seeds stored in the laboratory over 7, 30 and 78 days was 7, 12 and 19%. Thus, the 29% attrition after 1 year of burial was probably associated with a gradual loss of seed coat dormancy. Light levels (full sun and 25% full sun) manipulated with neutral density shade cloth had no significant influence on surface seed viability for either species.

Temperature and moisture interacted to influence *Leucaena* seed coat dormancy and embryo viability, but fluctuating temperatures under dry conditions affected neither viability nor germination. However, when moisture was available, germinability of seeds in the 40°C/20°C regime was higher (41%) than that of the control group maintained at 30°C (7%). All seeds in the 50°C/30°C regime imbibed water within 50 days, but none germinated. Low germination of buried seeds (29%) suggest that temperature/moisture combinations capable of disrupting seed coat dormancy or inducing embryo mortality were infrequent during the year of the field experiment.

Keywords: hardness; moisture, seedbank; shrubs; temperature; light; *Acacia berlandia*; *Leucaena pulverulenta*

Correspondence should be addressed to: M. K. Owens, Texas Agricultural Experiment Station, 1619 Garner Field Road, Uvalde, Texas, 78801, U.S.A.

Introduction

Seed dormancy can influence patterns of plant distribution, recruitment dynamics, and persistence in the plant community (Harper, 1977; Leck *et al.*, 1989). On the one hand, dormancy may be advantageous in that it enables seeds to accumulate in the soil seedbank and protects plants from expending their entire reproductive output at a given time (Koller, 1969). On the other hand, maintenance of seed dormancy when conditions are optimal for germination can be a disadvantage, as seeds are exposed to lethal environmental factors such as granivory and extreme temperatures for longer time periods.

Seed dormancy in leguminous plants is often associated with seed coat impermeability which prevents water uptake. The extent of seed coat-imposed dormancy (e.g. 'seed hardness') influences germinability and ultimately, seed longevity. Seed size, seed age, environmental conditions during ripening, and desiccation of mature seeds can affect the development of seed coat-imposed dormancy (Hyde, 1954; Quinlivan, 1971). Seeds of some leguminous species do not develop dormancy (*Trifolium subterraneum*, Quinlivan, 1971), whereas others exhibit partial dormancy (*Acacia senegal*, Cavanagh, 1980; *Desmodium* and *Lespedeza* spp., Martin *et al.*, 1975). Seeds of *Acacia* and *Prosopis* spp. with strong seed coat dormancy may persist in a viable state for decades (Tschirley & Martin, 1960; Cavanagh, 1980). Factors affecting seed coat dormancy and disruption of seed coat integrity would influence seedbank dynamics, temporal patterns of recruitment and the potential for plant re-establishment following disturbance.

When seed coats become permeable, viable seeds imbibe water and germinate if the temperature is suitable and moisture is available (Scifres & Brock, 1971). Rates of attrition from the seedbank are thus partially determined by factors influencing seed coat integrity. Breaking seed coat dormancy may be achieved by exposure to heat or radiation, soaking in acid or boiling water, or mechanical scarification (Quinlivan, 1971; Rolston, 1978). In nature, seed coat dormancy may be overcome by transit through the digestive tract of animals, abrasion, fire, high or fluctuating soil temperatures and microbial activity (Baskin & Baskin, 1989). These actions break dormancy by disrupting or softening the seed coat or by fracturing specialized tissues in the seed coat to allow water penetration.

In this study, we sought to quantify the extent of seed coat dormancy and seed persistence of two dryland leguminous shrubs, *Acacia berlandieria* and *Leucaena pulverulenta*, under field and controlled environment conditions. Both species are native to the Tamaulipan Biotic Province of southern North America and are potentially important sources of protein for wildlife and domestic livestock.

Materials and methods

Viability and germinability of seeds exposed to field and controlled environment conditions were compared to untreated seeds (controls) maintained under dry refrigeration at 5°C. Seed coat dormancy of untreated seeds was tested by placing 30 unscarified seeds at 30°C on saturated blotter paper for 7 days and recording the percentage of germination. Seeds which produced a 1 mm radicle were considered germinable. Seeds which did not germinate were tested for viability by mechanically scarifying the seed coat and returning the seed to the saturated blotter paper for an additional 7 days of observation. Scarified seed that did not produce a radicle was considered non-viable. In field trials, the number of seeds was counted at each date. Seeds which had softened, germinated or decomposed were considered as lost from the seed bank.

Controlled environment

The effects of temperature and moisture on *Leucaena* seed viability and germinability was assessed in a factorial experiment with two moisture (dry = no water added to blotter paper, wet = saturated blotter paper) and two diurnally fluctuating (14/10 h) temperature regimes (40°C/20°C, 50°C/30°C). These temperature fluctuations represent mean maxima and minima soil temperatures at a 3 cm depth in three microsites at a near-by study site during the period of natural seed fall (mid-July to August). Average relative humidities were 25%/75% during the 40°C/20°C experiment and 15%/30% during the 50°C/30°C experiment. *Acacia* seed was not tested because it did not exhibit dormancy (Everitt, 1983; Vora, 1989).

Temperature/moisture regimes were maintained for 60 days in two controlled environment chambers. For each temperature/moisture combination, 30 seeds were placed in each of 18 Petri dishes. The exception was the 30°C/50°C dry regime where 20 seeds per dish were used. The number of germinated seeds was recorded at 10-day intervals and three dishes (replications) were collected at random to test non-germinated seeds for viability. High imbibition and germination rates in wet treatments resulted in small sample sizes of ungerminated seed and consequently replicates were combined before analysis.

Field longevity

The longevity of unscarified *Acacia* and *Leucaena* seeds on the soil surface and at a depth of 3–5 cm was quantified in replicated livestock, deer, and rabbit-proof enclosures on the Silver Lake ranch, Kinney county, Texas (28° 19'N; 100° 25'W). Temperatures range from a mean daily maximum in July of 36°C to a daily minimum of 4°C in January. Mean annual rainfall of c. 500 mm is bimodally distributed with peaks in May and September. The enclosures were 8 km apart on a clayey, mixed, Thermic, Petrocalcic Paleustoll (site 1) and a clayey, montmorillonitic, Thermic, Lithic Petrocalcic Calciustoll (site 2). Average depths to the indurated layer were 15 and 25 cm at sites 1 and 2, respectively. Site 1 was dominated by a *Juniperus ashei*–*Quercus virginiana* parkland while site 2 was dominated by *J. ashei*–*Q. virginiana*–*Pinus cembroides* var. *remota*. Herbaceous zones between clusters or mottes of trees were dominated by the short statured perennial C₄ grasses, *Hilaria belangeri* and *Bouteloua trifida* on both sites. Twenty seeds per species were placed on the soil surface in each of 72 hardware cloth cages (8 × 8 cm; 0.7 cm mesh) designed to prevent losses to granivorous birds or rodents. Thirty-six cages were placed in each enclosure on 7 June, 1990. Half of the cages on each site were exposed to full sunlight and half were covered with fibreglass shade cloth to simulate photosynthetic photon flux densities (c. 25% full sunlight) and temperatures under *Junipers*–*Quercus* tree canopies. Three cages of *Acacia* seeds were randomly collected from each light environment on each site at 7-day intervals for 42 days. The design for *Leucaena* was similar except that collections were at 10-day intervals.

Buried seeds were enclosed in 6 × 6 cm fibreglass window screen bags and placed at a depth of 3–5 cm at random locations within the herbaceous zones of both sites. Seeds were buried on 1 July, 1989 during the time of natural seedfall. A sample of *Acacia* ($n = 144$) and *Leucaena* ($n = 200$) seeds was collected after 1.5 (16 August), 6 (28 December) and, for *Leucaena*, 12 (1 July 1990) months. The study was repeated in 1990 on seeds ($n = 200$ – 240) buried 1 June and collected after 1.5 (15 July) and 3.5 months (12 September).

The majority of buried *Acacia* seeds had degraded by the 1.5 month collection in 1989, thus a supplementary 3-month study on *Acacia* was conducted. Twelve bags (20 seeds per bag) were buried on 21 August 1989 on each site. Four bags from each site were collected at 30-day intervals and the viability of sound seeds determined.

Data analysis

Viability and germination of manipulated seeds were compared to that of control seeds using the χ^2 test of independence. The effects of environmental treatments on seed viability and germination in controlled environment and surface longevity studies were analysed using Categorical Data Analysis (CDA) which entails development of hierarchical loglinear models (Fienberg, 1985). Model selection was based on partitioning the likelihood ratio statistic (G^2), where the model with the fewest high order interactions and a non-significant p -value was the best-fit model. Explanatory variables in the controlled environment experiment included moisture, temperature, time (duration of exposure) and replication. The response variable was viability. Two separate analyses were conducted. The first analysis investigated viability in wet *vs.* dry regimes at two temperatures, and the second analysis investigated viability in the dry regime through time at two temperatures. This approach was used because of the rapid attrition of seeds in the wet moisture treatment which precluded the use of time and replications as explanatory factors in the CDA. Explanatory variables in the surface longevity study were time, light (shade *vs.* no shade) and replication. The response variable was viability. Assessing within-species survival was the main objective, so species were analysed separately.

CDA was not employed in the analysis of buried seed data because of different seed populations (1989 *vs.* 1990) and burial periods between years which confined model development to those providing information similar to independent χ^2 tests. Thus, buried seed data were analysed via independent χ^2 tests comparing buried and untreated seed viability and germination. Species were analysed separately as were years within species.

Results

Controlled environment

Temperature and moisture interacted significantly ($p < 0.001$, $\chi^2 = 711$, df. = 1) to affect seed coat dormancy and embryo viability of *Leucaena* seed. *Leucaena* seed coat dormancy under dry conditions was not significantly affected by temperature, time or replication ($\chi^2 = 76.4$, df. = 70) (Fig. 1(a and b)), and there were no significant differences in seed viability (97 *vs.* 93%, $\chi^2 = 0$, df. = 1) or germination (7 *vs.* 5%, $\chi^2 = 0.35$, df. = 1) between seeds maintained at constant 5°C and seeds experiencing fluctuating temperatures. However, under moist conditions, temperature significantly affected seed coat dormancy and viability ($\chi^2 = 614$, df. = 1). Viability within the 40°C/20°C temperature cycle was similar to viability of untreated seeds (96 *vs.* 97%, $\chi^2 = 0.1$, df. = 1) and significantly higher than that of seeds in the 50°C/30°C regime, where all seeds imbibed water, but none germinated (Fig. 1(c and d)). After 6 days of moist conditions at 40°C/20°C, 41% of the seeds germinated and 3% imbibed but failed to produce a radicle ($p < 0.001$, $\chi^2 = 55.6$, df. = 1). All remaining seeds germinated after mechanical scarification. Exposure to moist conditions and a 40°C/20°C temperature regime for 60 days increased germination from 7% (untreated seeds) to 41%.

Surface seed longevity

Shade, length of exposure and site had no significant effect on the number of viable *Acacia* ($\chi^2 = 130.0$, df. = 118) or *Leucaena* ($\chi^2 = 139.3$, df. = 142) seeds on the soil surface. *Acacia* seed viability was significantly reduced from 94 to 78% (188 from 240 seeds) after 7 days on the soil surface ($\chi^2 = 21.9$, df. = 1); there were no significant decreases during the next 35 days. For *Leucaena* seeds placed on the soil surface, 86% (1203 from 1398 seeds)

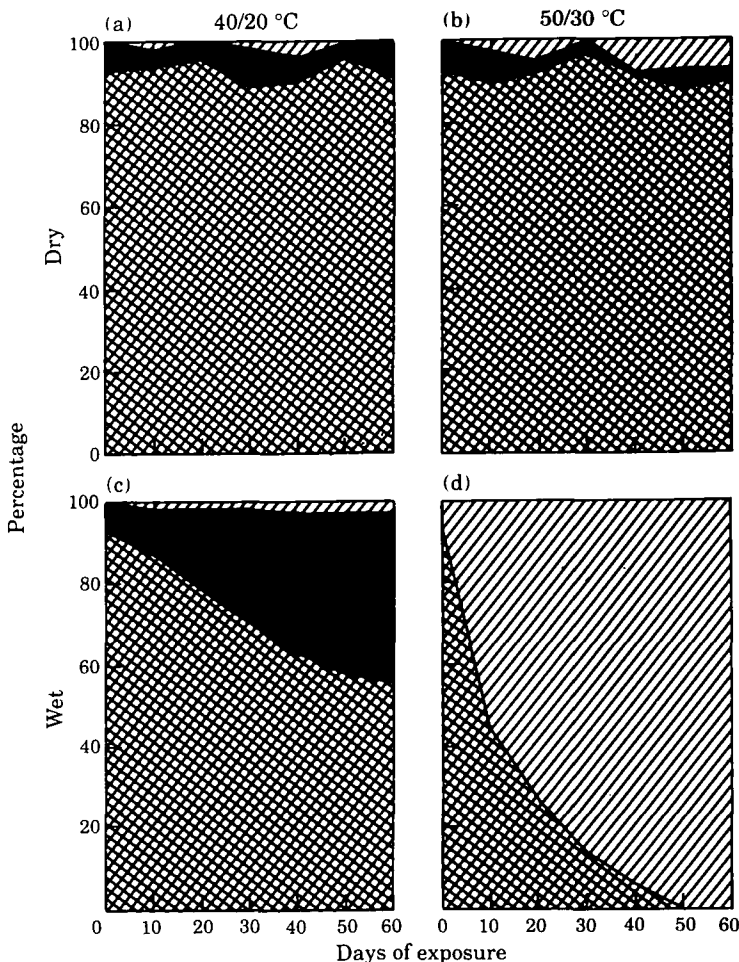


Figure 1. Fate of *Leucaena pulverulenta* seed during a 60-day controlled environment experiment with two moisture regimes (wet, dry) and two temperature regimes (40/20, 50/30°C). Seed fates were dormant and viable, \square ; germinated, \blacksquare ; and dead, \square .

were sound and viable at the end of the 60-day trial. This 14% attrition paralleled a 19% increase in germinability of laboratory seeds over the same time interval.

Buried seed longevity

In contrast to surface seeds, site differences in recovery of viable buried seed were significant for the non-dormant *Acacia* seed (Site 1 = 76%; Site 2 = 8%), but not for the dormant *Leucaena* seed. The site differences for *Acacia* were associated with differences in recovery after 1.5 months. Two weeks prior to burial, Site 1 received 1.6 cm of rain, whereas Site 2 received 3.8 cm. The low recovery of viable seeds on Site 2 after 1.5 months apparently reflected germination and decomposition in response to the higher soil moisture.

Viability of *Acacia* seeds prior to burial in July 1989 was 82% and attrition from the seed bank was 98% after 1.5 months (Fig. 2(a)). In the August 1989 burial trial, 80 of the 160 seeds disseminated (50%) had either germinated or decomposed within the first month.

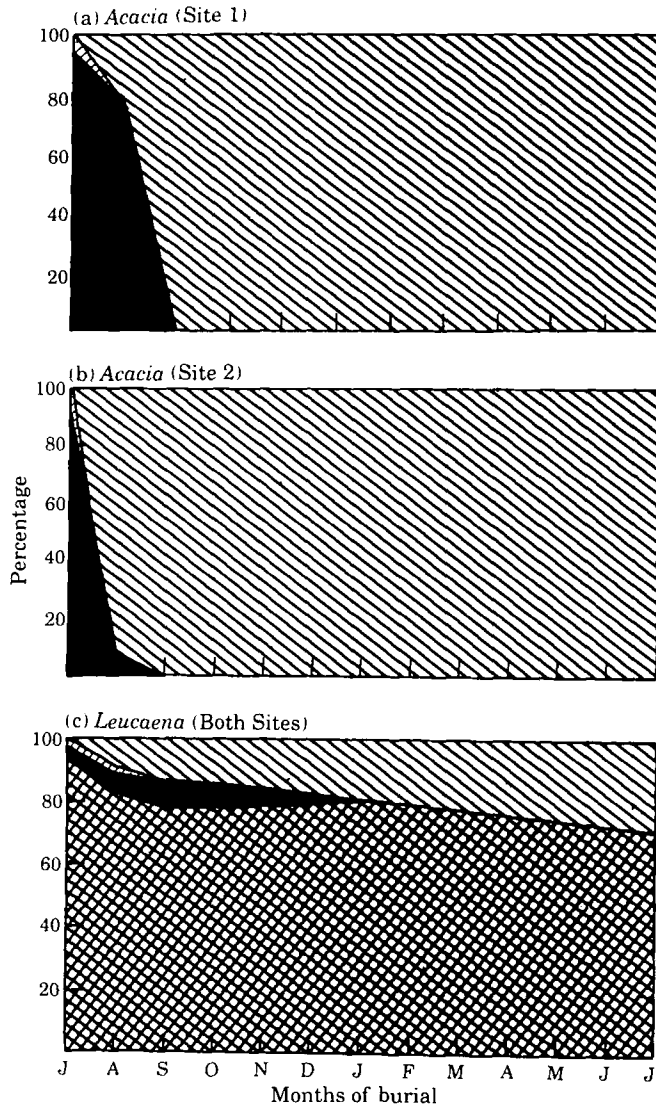



Figure 2. Fate of (a) *Acacia berlandieri* (Site 1), (b) *Acacia berlandieri* (Site 2) and (c) *Leucaena pulverulenta* seed buried at 3–5 cm depth in July 1989. Seed fates are as in Figure 1, with the addition of a decomposed state .

Of the remaining 80 sound seeds, 67 seeds (84%) were viable. After 2 months of burial no sound, viable seeds were recovered from the soil seedbank. Viability of the 1990 seedlot was 94% prior to dissemination. After 1.5 months of burial, 132 of the 240 seeds (55%) disseminated were recovered, whereas the remaining 45% had either germinated or decomposed in the soil. Only 86 of the 132 sound seeds recovered were viable (36% of the original population). No seeds buried longer than 3.5 months were sound or viable.

Leucaena seed was highly persistent and germination and viability were only slightly altered after 1.5 months of burial (Fig. 2(c)). Burial for 1.5 months had no effect on seed viability during 1989 ($\chi^2 = 1.0$, df. = 1) and only a slight effect (reduced from 97% to

83%) in 1990 ($\chi^2 = 7.8$, df. = 1). In 1990, 11% (22/200) of the seeds were found decomposed in the soil and 3% (6/200) imbibed water after scarification but did not germinate. An additional 7% (14/200 seeds) lost seed coat dormancy and germinated without scarification in the laboratory. Seventy-nine per cent of the original population (158/200 seeds) remained viable but dormant in the soil seed bank. Similar results were observed for the 240 *Leucaena* seeds buried in 1990. After 3.5 months of burial, 13% had germinated and/or decomposed in the soil, 1% imbibed water but did not germinate and 8% germinated without scarification. The remaining 188 seeds (78%) were sound and viable in the soil seedbank. The population of viable seeds after 6 months was not significantly different than after 3.5 months ($\chi^2 = 0.9$, df. = 1). For the 1989 seedlot, the population of sound, viable seeds in the soil seedbank was significantly ($\chi^2 = 20.3$, df. = 1) reduced to 71% of the original population after 12 months of burial. The other 29% (116/400 seeds) had germinated and/or decomposed in the soil.

Discussion

Seeds in natural communities are dispersed on the soil surface and gradually incorporated into the soil seed bank (Harper, 1977). An individual seed must therefore survive exposure on the soil surface until it is buried beneath either litter or soil and then survive underground until suitable conditions for germination occur. Differences in environmental conditions between the soil surface and subsurface can significantly influence seed survival. For example, seed survival of the biennial *Linum catharticum* was 99% after 3 years of burial (Pons, 1991) but only 15% after 2 years on the soil surface (Kelly, 1989). High evaporation rates from the soil surface in semi-arid environments typically cause germination on the soil surface to be moisture limited (Baskin & Baskin, 1989). Subsurface moisture at 3–5 cm depth may be slightly greater and seeds would have a higher probability of imbibing and germinating than would exposed seeds.

In the case of non-dormant *A. berlandieri* seeds, survival was dependent on whether the seed was buried or on the soil surface. While over 75% of the seeds survived 42 days of exposure on the soil surface, only 19% survived 42 days of burial. The lack of any dormancy mechanism suggests that these seeds would germinate whenever sufficient moisture was available. In our field trials, only 20% of the seeds on the soil surface germinated following 1 cm of precipitation. Most of the observed germination (over 75%) was from two cages, suggesting that seed placement in relation to microtopography and water movement may critically influence spatial patterns of germination after small rainfall events. *A. berlandieri* seeds on the soil surface were relatively more persistent than buried seeds, but only in microsites where conditions conducive to imbibition were infrequently realized. However, relative to buried seed, these surface seeds would be more apparent to granivores and subject to translocation to different microsites following large precipitation events (Wallace, 1991). As with surface seeds, differences in buried seed attrition on sites 1 and 2 during the first 1.5 months (Fig. 2) appear to have been influenced by slight differences in soil moisture. Germination of *A. berlandieri* thus appears to be spatially variable and triggered by rainfall events which can be too small to sustain seedling survival. These would impose significant constraints on the frequency and pattern of seedling recruitment. In contrast to *A. berlandieri*, *L. pulverulenta* exhibited seed coat dormancy and maintained dormancy on both the soil surface and subsurface. The loss of dormancy of buried seeds over time was similar to that of untreated seeds maintained in the laboratory.

The interactions between temperature and moisture can significantly affect seed germination of a wide range of semi-arid species (Scifres & Brock, 1969; Scifres & Brock, 1972; Briede & McKell, 1992). High temperatures, whether fluctuating or constant, do not affect many legume species under dry conditions. Seed coat dormancy of *Stylosanthes hamata*, an arid land improved-pasture legume, remained constant at 85 to 93% after 42 days of exposure when soil temperatures reached the mid-60°C level (McKeon & Mott,

1982). Cavanagh (1980) found that most seeds of Australian *Acacia* species were not affected by long-term exposure to high temperatures ($>50^{\circ}\text{C}$) under dry conditions. However, when moisture is present, seed response to temperature may be altered. A significant moisture-temperature interaction was observed for *L. pulverulenta* seeds in controlled environments, whereby seed coat dormancy was more affected under moist heat than dry heat (Fig. 1). In addition, fluctuating temperatures were more effective in reducing dormancy than were constant temperatures when moisture was present. The $50^{\circ}\text{C}/30^{\circ}\text{C}$ temperature regime, which would be representative of summer soil temperatures in herbaceous zones, caused 100% mortality when moisture was available. In contrast, attrition under the $40^{\circ}\text{C}/20^{\circ}\text{C}$ temperature regime, representative of under-tree canopies or spring/autumn conditions coincident with the bimodal pattern of precipitation in this area, was due to gradual loss of seed coat dormancy and subsequent germination rather than mortality. Attrition of surface or buried seed paralleled declines in dormancy observed for seeds stored in the laboratory at 30°C , suggesting that temperature/moisture combinations capable of disrupting seedcoat dormancy or inducing embryo mortality were infrequent during the year of the field experiment.

High mortality rates of buried *Acacia* seeds coupled with the spatial patterns of mortality for surface seeds suggests that high levels of annual seed production may be necessary for *Acacia berlandieri* to reproduce successfully and to persist in environments which experience periodic disturbances (e.g. fire, drought, frost, etc.). The ability of this species to sprout vigorously after disturbance (Bozzo *et al.*, 1992) somewhat alleviates the need for a persistent seedbank, but catastrophic disturbances that cause high adult mortality could lead to local extinction (Fulbright & Beasom, 1987). *Leucaena pulverulenta*, on the other hand, would produce a more persistent seed bank so annual seed production would be less critical to ensure continued presence in the community.

The authors would like to thank J. R. Reynolds and E. de la Garza for assistance in field data collection. Tim Fulbright made helpful suggestions on an earlier draft. Research was supported by the Texas Agricultural Experiment Station Projects H-6995 and H-6717 and the Moody Foundation of Galveston, Texas. This paper is published with the approval of the Director, Texas Agricultural Experiment Station as technical publication TA-31032.

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